

LIGHT ATTENUATION IN THE WATER COLUMN IN CHASCOMUS POND (ARGENTINA)

ATENUACION DE LA LUZ EN LA COLUMNA DE AGUA EN LA LAGUNA DE CHASCOMUS (ARGENTINA)

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ABSTRACT

The depth of the euphotic zone in Chascomús Pond fluctuated around 54 cm, and the average of the Secchi disk reading was 19 cm, with a relative light intensity at this depth of 15.9 %. The seston and chlorophyll-a concentrations had significant relationship with water transparency ($P < 0.01$). Extinction coefficient showed a range from 1.8 to 11.1 m^{-1} (mean 6.1 m^{-1}), during winter and summer respectively; these values, may be attributable to the absorption due to suspended living and nonliving particles, being the mean annual value of seston 182.3 $mg.l^{-1}$, with an extreme value in October of 1020.1 $mg.l^{-1}$. Transparency (Z_{sd}) and extinction coefficient (K) relationship showed the pattern of $Z_{sd} = n / K$, for which the constant was 2.04 ($P < 0.01$). Primary production rate fluctuated between 28.5 and 517.9 $mg C.m^{-3}h^{-1}$, and the light utilization efficiency by phytoplankton community was high with a mean value of 32%, due to the absorption of light by the suspended particles that leads to a low photosynthetically available radiation for the primary producers. These light field conditions, transparency, euphotic depth and extinction coefficient, were strongly related to the suspended particulate matter due to the morphometry of this shallow pond and the dominant winds, that prevent sedimentation thus decreasing light penetration in the water column.

KEYWORDS: Light extinction coefficient, primary production, photosynthetic efficiency, suspended particulate matter, vertical mixing, Chascomús, Argentina.

RESUMEN

La profundidad del estrato eufótico, en la Laguna de Chascomús, fluctuó alrededor de los 54 cm, siendo el promedio del disco de Secchi de 19 cm, con una radiación relativa incidente en esa profundidad de 15.9%. Se analizó la correlación entre la transparencia el seston y la concentración de clorofila-a, siendo ambas significativas ($P < 0.01$). El coeficiente de extinción de la luz fluctuó entre 1,8 y 11,1 m^{-1} durante el invierno y verano, atribuyéndose dichos valores a la absorción ocasionada por la cantidad de partículas en suspensión, siendo el valor promedio del seston de 182,3 $mg.l^{-1}$, con un valor extremadamente elevado en primavera de 1020,1 $mg.l^{-1}$. Al resolver la relación entre la transparencia (Z_{sd}) y el coeficiente de extinción (K) bajo la forma $Z_{sd} = n / K$, se halló una constante de 2,04 ($P < 0,01$). La tasa de producción primaria fluctuó entre 28,5 y 517,9 $mg C.m^{-3}h^{-1}$, con una elevada eficiencia fitoplanctónica en la utilización de la luz ($\bar{\epsilon} = 32\%$), interpretándose a este valor como adaptación de la comunidad algal a la baja intensidad de luz recibida. Las condiciones de luz subacuática, caracterizadas por el disco de Secchi, estrato eufótico y coeficiente de extinción, guardan una buena correlación con el material particulado en suspensión. La morfometría de la laguna y régimen de vientos contribuyen a la resuspensión de sedimentos del fondo, disminuyendo la penetración de la luz en toda la columna de agua y condicionando la intensidad lumínica disponible para el fitoplancton en los diferentes niveles del estrato eufótico.

PALABRAS CLAVES: Coeficiente de extinción de la luz, producción primaria, eficiencia fotosintética, material particulado en suspensión, mezcla vertical, Chascomús, Argentina.

INTRODUCTION

The evaluation of transfer efficiencies of solar energy among and within trophic levels is the interest in limnological studies. The fraction of sunlight stored through photosynthesis is one of

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the most relevant process for the maintenance of the structural and functional integrity of individual organisms and aquatic ecosystems. An important aspect for comparing water bodies is the estimation of the ratio of total primary productivity in the water column in relation to the light energy that penetrates the surface, that is to say light utilization efficiency.

The light attenuation in the water column depends on the spectral composition of light (Kirk, 1979; Atlas & Bannister, 1980; Marra & Heinemann, 1982), yellow substances (Kirk, 1976; Bricaud *et al.*, 1981), nonalgal particulate matter (Arai, 1981), in addition to taxonomic composition of the algal community, phytoplankton physiology (Welschmeyer & Lorenzen, 1981; Falkowski, 1984), cell size and geometry (Kirk, 1983).

The objective of this study was to evaluate the influence of the suspended particulate matter and pigment concentrations on the rate and photosynthetic efficiency of the phytoplankton. With this purpose the light attenuation in the water column, the extinction coefficient, the Secchi disk readings, primary production rate and depth of the euphotic zone were measured in Chascomús pond.

MATERIALS AND METHODS

Chascomús pond is located in the Province of Buenos Aires (35° 36'S, 58° W). It belongs to the basin area of the Salado River, which is situated in the geomorphological unit called Pampa deprimida (Frenguelli, 1950). It is a shallow ecosystem, rich in nutrients, alkaline and with high values of suspended particulate matter and soluble humic substances (Conzonno & Fernandez Cirelli, 1988). Geomorphological details can be obtained from Dangavs (1976), chemical and biological features are given in Conzonno & Claverie (1990) and Romero & Arenas (1990).

Samples were collected monthly in a central station. The transparency was determined by the Secchi disk depth (Z_{sd}); the intensity of incident light on the surface ($I_{0, m}$) and at each 10 cm in the water column, were measured with a photometer-radiometer quantum Li-Cor 192 SB.

The primary production rates were measured by the dissolved oxygen technique (clear and dark bottles), in an integrated sample of the euphotic zone, using a 2 litre 0.5 m long Van Dorn bottle. The analyses were performed according to

Winkler method, in duplicate, with a precision of about $\pm 0.05 \text{ mg.l}^{-1}$; then the results were converted to carbon values by means of the photosynthetic quotient 1.2 (Strickland & Parson, 1960). The primary production measurements were carried out in the laboratory at light saturation, for a period of 4 hours.

Chlorophyll-a concentrations were determined spectrophotometrically, using acetone 90% as solvent, following the technique of Golterman (1971). The suspended particulate matter, seston, was obtained by weighting the residue resulting from the filtration of appropriate volumes through Whatman GF/C, previously treated at 500 °C.

Light attenuation in water column was calculated every 10 cm, by the Lambert-Beer formula, and the extinction coefficient was obtained by the following equation $K = -\ln(I_z / I_0) / z$. The sensor measures the intensity and energy of photosynthetic available radiation (PAR), therefore the extinction coefficient corresponds to this fraction of the solar spectrum (390-710 nm), evaluated according to the following equation (Dubinsky & Berman, 1979):

$$K = \frac{-\ln(\text{PAR}_{z_2} / \text{PAR}_{z_1})}{z_1 - z_2}$$

Light utilization efficiency was calculated taking into account the relation suggested by Dubinsky (1980):

$$E = \frac{\text{PSR}}{\Delta \text{PAR}_z \Delta z} \cdot 100\%$$

PSR is the photosynthetic stored radiation (Morel, 1978), obtained by means of primary production measurements converted to $\text{cal.m}^{-3}.\text{h}^{-1}$ using a factor of 12 cal. (mg C)⁻¹ (Margalef, 1983).

ΔPAR_z is the photosynthetic available radiation, between z_1 and z_2 levels (Δz); it is the energy absorbed by the euphotic depth, calculated by difference between PAR_{z_1} (downwelling irradiance on the top) and PAR_{z_2} (irradiance corresponding to the bottom of the photic zone). Finally $\Delta \text{PAR}_z \Delta z^{-1}$ was converted to $\text{cal.m}^{-3}.\text{h}^{-1}$ using a factor of and 41.6 cal. (μE)⁻¹ (685 nm; Margalef, 1983).

RESULTS AND DISCUSSION

As the phytoplanktonic photosynthesis depends mainly on the natural light regimen, we analyzed the photosynthetic available radiation profiles (PAR) according to depth (Fig. 1). Schanz (1985) showed five characteristic light-depth curves in relation to vertical mixing of water levels, phytoplanktonic density and amount of suspended particulate matter accumulated at different depth.

According to this classification the months of June, July, January, March and May-1989 fit the type (I), since natural logarithms of light intensity at each depth showed a nearly straight line. This is due to vertical mixing that caused an homogeneous distribution of algal and nonalgal components. During October we observed a similar response to curve type (II), with two layers with different light absorption properties. The months of September, December and February fit the type (IV), since they indicated a low extinction coefficient in the surface region and a higher one in the underlying water mass, linked to the temporary calm and the increase of suspended particulate matter in the lower stratum. The curve of April, May-1988 and November fit the type (V), with two inflection points due to the appearance of three different layers in the water column.

The depth of the euphotic zone, 1% of incident light, fluctuated around 54 cm and it was similar to the one observed in 1984-1985 (Conzonno & Claverie, 1987/1988), except for October 1988 with only 27 cm depth, in accordance with seston (1020.1 mg.l⁻¹) and chlorophyll-a (204.6 µg chlor.l⁻¹). These concentrations were the highest for both variables throughout the year. On the contrary, in March 1989, a 124 cm euphotic zone was observed in accordance with low values of suspended particulate matter (26.8 mg.l⁻¹) and unusual calm weather conditions.

Depth profiles of relative intensity (1/I₀) are given in figure 2. Except for the period February- March, the rest of the year had an almost similar behaviour. Arai (1981) calculated the relative light intensity that penetrates at each layer as a comparative parameter in different water bodies. He obtained for the turbid lake Suwa at about 0.40 m depth for 1% I/I₀. The results of the Chascomus pond were similar to the turbid lake cited above, since 1% I/I₀ was observed at about 50 cm, except on March 1989.

For many authors transparency versus relative light intensity relationship is a straight line, and at the depth of the Secchi disk reading the 1/I₀ averages 10%; Birge & Juday (1929) determined a value of 5%; Ichimura (1956) obtained a percentage of 15%; Tsuda (1980) found 15 to 27% (average 22%); Mariazzi *et al* (1991) presented values between 10 and 25%. The average of the Secchi disk reading was 19 cm which corresponds to 15.9% of relative light. It is important to note that for the lowest Secchi disk reading, 10 cm, observed in October, the percentage of relative light received at that depth was 22.8%; and for the highest Secchi reading 35 cm, in March 1989, a similar relative light percentage was observed (28.3%).

The relation between the transparency and the chlorophyll-a content is usually expressed as:

$$Z_{sd} \cdot a \text{ (chlor.)}^b = a$$

where Z_{sd} Secchi disk readings
(chlor) chlorophyll-a concentrations
a and b constants

Shapiro *et al.* (1975) got values for a and b constants of 7.7 and 0.68 respectively; while Rull *et al.* (1984) found values of 3.5 and 0.17. In Chascomus pond we found the constants a = 7.4 and b = 0.27 (P < 0.01, Fig. 3a). On the other hand, similar relationship was observed between seston and the transparency (P < 0.01, Fig 3 b), $Z_{sd} \cdot (\text{seston})^{0.33} = 4.5$.

The extinction coefficient of the photosynthetically available radiation showed a mean value of 6.1 m⁻¹, with a minimum of 1.8 m⁻¹ during March 1989, and a maximum of 11.1 m⁻¹, in October 1988. These seasonal variations coincided with the one corresponded to the suspended particulate matter, whose values were 26.8 and 1020.1 mg.l⁻¹, respectively. The above mentioned coefficient usually given to other water bodies are lower; 0.25 - 1.31 m⁻¹ for Lake Biwa (Nakanishi, 1976); 0.90- 4.20 m⁻¹ for Rio Tercero Dam (Romero *et al.* 1988); 0.23-0.69 m⁻¹ for Ramos Mexia Dam (Mariazzi *et al.* 1991). In a previous study a mean coefficient of 9.6 m⁻¹ was reported for this pond, by Conzonno & Claverie (1987/1988).

Comparing the extinction coefficient with the photosynthetic pigment concentrations, Bindloss (1976) and Robarts (1979) presented K values between 1 to 3 m⁻¹ for Lake Leven and Lake Mc Il-

waine respectively, with chlorophyll-a concentrations from 100 to 500 (ug chlor. l⁻¹; Ganf & Viner (1973) reported from Lake George (Uganda) an extinction coefficient K changed from 2 to 20 m⁻¹, with pigment contents from 200 to 1000 ug chlor.l⁻¹. In this study K fluctuated from 1.8 to 11.1 m⁻¹, and chlorophyll-a concentrations from 18.5 to 204.6 (ug chlor. l⁻¹; and also higher coefficient were observed simultaneously with lower chlorophyll-a values (Table I). These results suggested that the underwater light attenuation depended mainly on the suspended particulate matter.

The relation between the transparency and the extinction coefficient is shown in the following equation $Z_{sd} = n / K$. The value of the constant n was considered by Rull *et al.* (1984) to be from 0.6 to 2.3 (average 1.75); Romero *et al.* (1988) found 1.28 at the Rio Tercero Dam (Argentina). It is considered that a value near to 1.7 (Planas, 1973) is the most appropriate one. Limnologists usually take the value 2.3. The relationship between the transparency and K for this pond was 2.04 (P < 0.01).

Phytoplankton primary production showed a clear seasonal variations, with higher values during February (517.9 mg C.m⁻³.h⁻¹) and October (402.5 mg C.m⁻³.h⁻¹), and lower ones in winter (28.5 mg C.m⁻³.h⁻¹). While the average winter primary production was 181.5 mg C. m⁻³. h⁻¹, the summer average was 377.5 mg C. m⁻³.h⁻¹ (Fig. 4).

Light utilization efficiency, E (Dubinsky & Berman, 1981), showed an average value of 32%, and ranged from 4 to 88%. Although in most studies the efficiency reached only 30% (Talling, 1982; Dubinsky & Schanz, 1984), it had been observed that in some occasions this theoretical limit was exceeded (Tilzer *et al.* 1975; Bannister & Weidemann, 1984). Variations in light intensity due to the absorption by seston may influence physiological responses: superimposed on these variations are variations induced by turbulent mixing (Falkowski & Wirick, 1981). It was also noted that an adaptation to fluctuating light regimes resulted in an increased photosynthetic capacity and efficiency (Frechette & Legendre, 1978; Walsh & Legendre, 1982). Therefore our high efficiency values might be due to the response of algae population to the low light intensity in this pond, suggesting that the phytoplankton population was shade-adapted. This increase resulted from a combination of low near-surface light that reduces the

denominator in the efficiency equation.

It was observed that the primary production and the photosynthetic efficiency had similar seasonal variation; high rates of photosynthesis such as the ones observed in October and February fit the higher light utilization efficiency. These results may be connected with low PAR values as a consequence of the high concentration of seston.

CONCLUSIONS

Seston is the prevailing factor that conditioned the attenuation of light in this pond thus accounting for the low values of the Secchi disk readings, as well as for the depth of the euphotic zone and high values of the extinction coefficient.

The suspended particulate matter is related to the regime of predominant winds and morphometry of this shallow pond, so that the constant vertical mixing maintains the particles in suspension in the water column, preventing the sedimentation and reducing the light penetration.

As a consequence the primary production was restricted to the subsurface and the light utilization efficiency was high since an important fraction of the incident radiation was absorbed by the suspended particulate matter.

REFERENCES

- ARAI, T. 1981. Attenuation of incident solar radiation in Lake water. *Jap. T. Limnol.* 42 (2): 92-99.
- ATLAS, D. & T.T. BANNISTER. 1980. Dependence of mean spectral extinction coefficient of phytoplankton on depth, water colour, and species. *Limnol. Oceanogr.* 25: 157-159.
- BANNISTER, T.T. & A.D.WEIDEMANN. 1984.The maximum quantum yield of phytoplankton photosynthesis in situ. *J. Plankton Res.* 6: 275-294
- BINDLOSS, M.E. 1976. The light-climate of Lake Leven a shallow Scottish lake, in relation to primary production by phytoplankton. *Freshwat. Biol.* 501-518.
- BIRGE, E.A. & C. JUDAY. 1929. Transmission of solar radiation by the waters of inland lakes. *Trans Wisconsin Acad. Sci., Art. and Let.* 24: 509-580.
- BRICAUD, A., A. MOREL & L.PRIEUR. 1981. Absorption by dissolved organic matter of the sea (yellow substances) in the UV and visible domains. *Limnol. Oceanogr.* 26: 43-53.
- CONZONNO, V.H. & E.F. CLAVERIE. 1987/1988. Phytoplankton primary production in Chascomús Pond (Provincia de B.A., Argentina). *Ecosur*

- 14/15 (25/26): 7-16.
- , 1990. Chemical characteristics of the water of Chascomus pond (Prov. de B.A.) Limnological implications. *Rev. Brasil. Biol.* 50 (1): 15-21.
- CONZONNO, V.H. & A.FERNANDEZ CIRELLI. 1988. Soluble humic substances from Chascomus pond (Argentina). *Arch. Hydrobiol.* 109: 305-314.
- DANGAUS, N.V. 1976. Descripción sistemática de los parámetros morfométricos considerados en las Lagunas Pamfásicas. *Limnol. I, fasc. 2*: 35-39.
- DUBINSKY, Z. 1980. Light utilization efficiency in natural phytoplankton communities. In *Primary productivity in the Sea*, Ed. P.G. Falkowski-New York Res: 83-97.
- DUBINSKY, Z. & T. BERMAN. 1979. Seasonal changes in the spectral composition of downwelling irradiance in Lake Kinneret (Israel). *Limnol. Oceanogr.* 24 (4): 652-663.
- , 1981. Photosynthetic efficiencies in aquatic ecosystems. *Verh. Int. Ver. Limnol.* 21: 237-243.
- DUBINSKY, Z. & F. SCHANZ. 1984. Field experiments for in situ measurements of photosynthetic efficiency and quantum yield. *J. Plankton Res.* 6: 339-349.
- FALKOWSKI, P.G. & C.D. WRICK. 1981. A simulation model of the effects of vertical mixing on primary productivity. *Mar. Biol.* 65: 69-75.
- FALKOWSKI, P.G. 1984. Physiological response of phytoplankton to natural light regimes. *J. Plankton Res.* 6 (2): 295-307.
- FRENCHETTE, M. & L. LEGENDRE. 1978. Photosynthese phytoplanktonique: response a un stimulus simple imitant les variations de la lumiere engendrees par les ragues. *J. Exp. Mar. Biol. Ecol.* 32: 15-25.
- FRENGUELLI, T. 1950. Rasgos generales de la morfología y la geología de la Prov. de B.A. *Publ. LEMIT Sec. 2* (33): 1-18.
- GANF, G.G. & A.B. VINER. 1973. Ecological stability in a shallow equatorial lake (Lake GEORGE (Uganda). *Proc. R. Soc. B.* 174:321-346.
- GOLTERMAN, H.L. 1971. Methods for chemical analysis of Fresh Water. IBP Handbook N. 8 Blachswell Scientific Publications, Oxford. 172 pp.
- ICHIMURA, S. 1956. On the ecological meaning of transparency for the production of matter in phytoplankton community of Lake. *Bot. Mag., Tokio* 69: 219-220.
- KIRK, J.T.O. 1976. Yellow substance (gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Aust. J. mar. Freshwat. Res.* 27: 61-71.
- , 1979. Spectral distribution of photosynthetically active radiation in some south-eastern Australian waters. *Aust. J. mar. Freshwat. Res.* 30: 81-91.
- , 1983. Light and photosynthesis in aquatic ecosystems. Cambridge, University Press.
- MARGALEF, R. 1983. *Limnología*. Ed. Omega. Barcelona. 1010 pp.
- MARIAZZI, A.; V.H. CONZONNO; R. ECHENIQUE & H. LABOLLITA. 1991. Physical and chemical characters, phytoplankton and primary production of Ezequiel Ramos Mexia Reservoir (Argentina). *Hydrobiologia* 209: 107-116.
- MARRA, J. & K. HEINEMANN. 1982. Photosynthesis response by phytoplankton to sunlight variability. *Limnol. Oceanogr.* 27 (6): 1141-1153.
- MOREL, A. 1978. Available, usable and stored radiant energy in relation to marine photosynthesis. *Deep. Sea Res.* 25: 673-688.
- NAKANISHI, M. 1976. Seasonal variations of chlorophyll-a amounts, photosynthesis and production rate of macro and micro phytoplankton in Shiozu Bay, Lake Biwa. *Physiol. Ecol. Teapan* 17: 535-549.
- PLANAS, M.D. 1973. Composición, ciclo y productividad del lago de Bañolis. *Oecologia aquatica*: 113-106.
- ROBARTS, R.D. 1979. Underwater light penetration, chlorophyll and primary production in a Tropical African lake (Lebe Mc Ilwaine, Rhodesia). *Arch. Hydrobiol.* 86: 423-444.
- ROMERO, M.C.; A.A. MARIAZZI & P. ARENAS. 1988. Condiciones de luz subacuática como factores determinantes de la eficiencia fotosintética fitoplanctónica. Embalse del Río Tercero (Prov. Córdoba, Argentina). *Oecologia aquatica* 9: 1-8.
- ROMERO, M.C. & P. ARENAS. 1990. Aporte relativo de diferentes fracciones fitoplanctónicas a la producción primaria y concentración de clorofila, en la laguna de Chascomús (Prov. B.A., Argentina). *Rev. Brasil. Biol.* 50 (2): 327-333.
- RULL, V., T. VEGAS & T. NAVARRO. 1984. Extinción de la luz en los embalses españoles. Relaciones con la concentración de clorofila y las partículas en suspensión. *Oecologia aquatica* 7: 25-36.
- SCHANZ, F. 1985. Vertical light attenuation and phytoplankton development in Lake Zurich. *Limnol. Oceanogr.* 30 (2): 299-310.
- SHAPIRO, J.J.; B. LUDQUIST & R.E. CARLSON. 1975. Involving the public in Limnology. An approach to communication. *Verh. Int. Verlin. Limnol.* 19: 866-874.
- STRICKLAND, T.D.H. & T.R. PARSON. 1960. A manual of sea water analysis. Fisheries Res. Board of Canada. Ottawa. 310 pp.
- TALLING, J.F. 1982. Utilization of solar radiation by phytoplankton, in Helene, *et al.* eds. *Trends in Photobiology*, Plenum Press, New York & London: 619-631.
- TILZER, M.M.; C.R. GOLMAN & E.DE AMEZAGA. 1975. The efficiency of light energy utilization by lake phytoplankton. *Verh. int. Verein. Limnol.* 19: 800-807.
- TSUDA, R. 1980. Measurements of underwater spectral irradiance in Lake Biwa. *Jap. J. Limnol.* 41 (2): 57-67.
- WALSH, P. & L. LEGENDRE. 1982. Effets des fluctuations rapides de la lumiere sur la photosynthese du phytoplankton. *J. Plankton Res.* 4: 313-327.
- WELSCHEMEYER, N.A. & C.J. LORENZEN. 1981. Chlorophyll-specific photosynthesis and quantum efficiency at subsaturating light intensities. *J. Phycol.* 17: 283-293.

TABLE I. Seasonal variations of the studied parameters.

	25-IV	23-V	22-VI	27-VIII	6-IX	4-X	10-X	15-XI	26-I	23-II	21-III	6-V
PP	204.1	182.1	334.9	161.1	178.3	402.5	270.3	276.1	277.9	517.9	280.5	28.5
mgC.m ⁻³ .h ⁻¹	18.6	37.2	34.6	33.7	22.6	204.6	38.6	32.5	25.2	68.7	31.9	18.5
Chlor-a	62.1	72.3	84.5	117.5	166.5	1020.1	180.5	79.5	39.1	156.1	26.8	
ug chlor-l	20	20	15	15	15	10	15	15	28	15	35	27
Secchi	500	500	450	750	900	350	1050	840	1100	750	600	450
cm	43	40	33	90	110	82	115	220	160	150	170	93
Io, m	8.6	8.1	7.3	12.1	12.2	22.8	10.9	26.2	14.5	20.1	28.3	20.6
uE.m ⁻² .s ⁻¹	55	44	43	38	49	27	40	60	51	48	124	68
I _{sd}	4.8	7.2	6.6	7.2	7.5	11.1	7.2	3.6	5.4	7.1	1.8	3.6
uE.m ⁻² .s ⁻¹	31	26	57	16	15	88	20	25	19	53	36	4
I _{sd} /I _o , m												
%												
Z, l%												
cm												
K												
m-l												
E												
%												

PP: primary production rates; Chlor-a: chlorophyll-a concentrations; I_o, m: sub-surface light intensity; I_{sd}: light intensity at Secchi disk depth; I_{sd}/I_o, m: relative light intensity at Secchi disk depth; Z, l%: euphotic depth; K: extinction coefficient; E: light utilization efficiency.

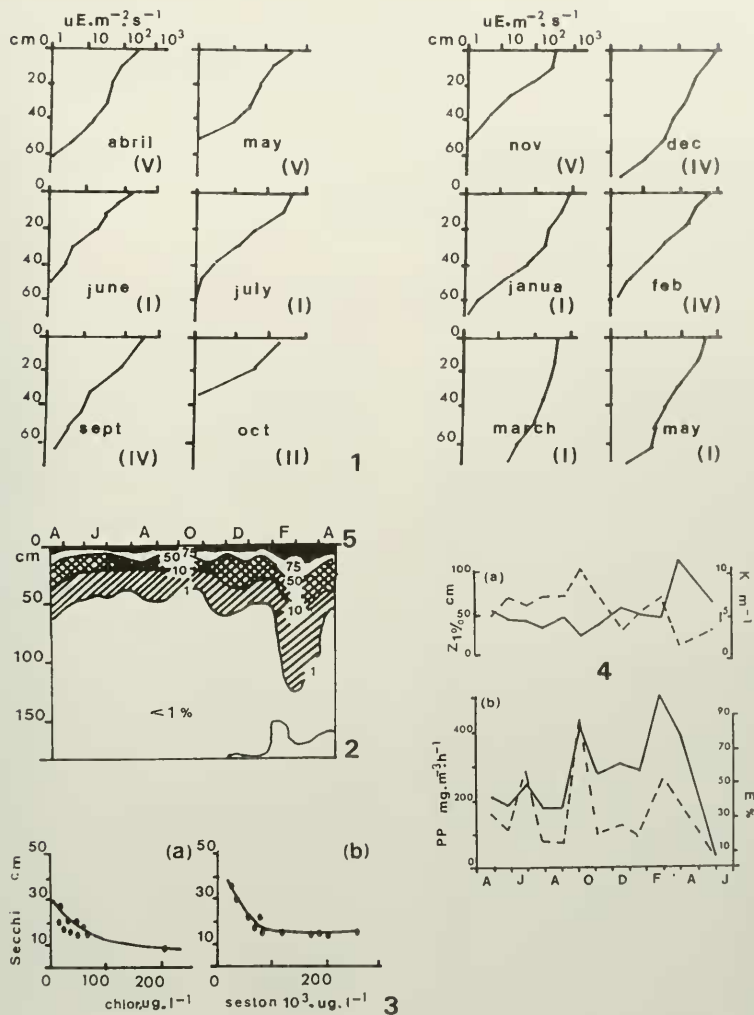


FIGURE 1. Photosynthetic available radiation (PAR) profiles ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (Roman numbers refer to types light-depth curves). FIGURE 2. Vertical profile of relative light intensity ($I/I_0\%$). FIGURE 3. Relationship between Secchi disk readings and (a) Chlorophyll-a concentrations; (b) Seston. FIGURE 4. (a) Seasonal variation of the euphotic depth (—, $Z_{1\%}$ cm); and the extinction coefficient (----, $K\text{m}^{-1}$); (b) light utilization efficiency (-·-·-, $E\%$) and primary production (—, PP - $\text{mg}\cdot\text{C}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$).